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DYNAMICS OF SINGLE-SPECIES POPULATION GROWTH: STABILITY OR CHAOS?[1]

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Abstract. We have examined stability at the carrying capacity for 25 genetically different populations of *Drosophila melanogaster*. In spite of their genetic heterogeneity, 20 of the populations yield stable equilibria and none have eigenvalues significantly greater than one. Computer simulations demonstrate how selection at the individual level may account for population stability (and, hence, that group selection is not necessary for the evolution of stability). Recent theoretical studies on density-dependent selection in random environments provide predictions consistent with our empirical findings.

Key words: computer simulations; density-dependent selection; Drosophila melanogaster; *evolution; serial transfer system.*

INTRODUCTION

Much attention has recently been devoted to the complex behavior generated by discrete models of density-dependent population growth (May 1974, May and Oster 1976, Guckenheimer et al. 1977). Certain models predict that, within specific ranges of parameter values, populations will not exhibit stable equilibrium points but rather stable cycles or chaotic behavior indistinguishable from a stochastic oscillation. Guckenheimer et al. (1977) have further shown how the apparent chaotic behavior may actually be a set of points called a strange attractor. In such cases, population size can be described only in a statistical sense, i.e., in terms of an observed average value.

The crucial issue is whether these findings are at all relevant to the dynamics of natural populations. Most natural and laboratory populations exhibit some sort of fluctuation about their carrying capacity. It is generally assumed that these fluctuations are largely due to extrinsic factors, such as resource availability or weather conditions, rather than some intrinsic property of the density-regulating mechanism.

Hassell et al. (1976) have concluded that chaotic or cycling dynamics in nature must be rare; their results are based on estimates of the parameters from a single first-order difference equation. Guckenheimer et al. (1977) have questioned such a conclusion, because they have found that more realistic models of population growth, such as those that include overlapping generations, are more likely to exhibit complex behaviors.

In this study we examine the stability at the carrying capacity of populations of *Drosophila melanogaster* in a serial transfer system. We will not attempt to distinguish populations with cycling dynamics from those showing chaotic dynamics. Instead, we will distinguish populations that have asymptotically stable carrying capacities from those with either cyclic or chaotic dynamics. The serial transfer system represents a more complex and "natural" system of population maintenance than a single-generation discrete regime. Our method of analysis makes it possible to determine the linear dynamics near the carrying capacity from empirical observations, without assuming any specific underlying model. We study a number of genetically different populations in order to determine whether the stability of a population is affected by the population's genetic composition.

METHODS

Drosophila melanogaster were collected at Strawberry Canyon, Berkeley, California. A total of 49 lines, each homozygous for a different second chromosome, was obtained by standard procedures (Tracey and Ayala 1974). From these 49 populations, 24 nonlethal, nonsterile lines were selected for this study. A random heterozygous line (H) was also obtained by intercrossing the 24 homozygous lines.

The population dynamics in the serial transfer system were determined in the following fashion (Mueller and Ayala 1981*a*): A specified number of adults were introduced in a culture and allowed to lay eggs for 1 wk. For each line, we used two densities, one above and the other below the carrying capacity of the line. After 1 wk of egg laying, the surviving adults were counted. The number of emerging adults from each culture were counted and discarded at weekly intervals for the next 3 wk. The densities at which these experiments were carried out, the carrying capacity, and the total number of replicates for each population are shown in Table 1. The carrying capacity is the least-squares estimator from the theta model, $N_{t+1} = N_t[1 + r(1 - (N_t/K)^\theta)]$ (see Mueller and Ayala 1981*a*).

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As explained in Mueller and Ayala (1981*a*), the number of adults, N_t, in the serial transfer system can be expressed as

$$N_t = f_1(N_{t-1}) + f_2(N_{t-2}) + f_3(N_{t-3}) + f_4(N_{t-4}), \quad (1)$$

where each $f_i(N_{t-i})$ is some unknown function which relates the number of adults emerging (or surviving, in the case of f_1) in an i-wk-old culture to the number that laid eggs in that culture.

To determine the approximate linear dynamics around the carrying capacity a linear version of Eq. 1 is used:

$$N_t = (a_1 + b_1N_{t-1}) + (a_2 + b_2N_{t-2}) + (a_3 + b_3N_{t-3}) + (a_4 + b_4N_{t-4}). \quad (2)$$

This is a nonhomogeneous fourth-order linear difference equation. The carrying capacity can be determined from Eq. 2 to be $\Sigma_i a_i/(1 - \Sigma_i b_i)$. If the modulus of the largest eigenvalue of Eq. 2 is less than one, then perturbations away from the carrying capacity will asymptotically diminish towards zero.

In practice the modulus of the largest eigenvalue is estimated, by a method called the jackknife (Mueller and Ayala 1981*a*), as the mean of m approximately independent and identically distributed random variables that are called pseudovalues. Briefly, the jackknife method is as follows: Given a set of m replicate experiments, the jth replicate is deleted and the largest eigenvalue is calculated with the remaining data. This process yields a set of m pseudovalues, the mean of which is the jackknifed estimate of the largest eigenvalue. The pseudovalues are also used to estimate the variance of the largest eigenvalue and are used in a one-way analysis of variance. The one-way analysis of variance gives an indication of the degree of heterogeneity with respect to stability among the 25 genetically different populations.

There is an important difference between our stability analysis and the method commonly used (Hassell et al. 1976). Usually, it is assumed that a certain nonlinear function adequately predicts the population dynamics. This nonlinear function is then approximated by a linear function derived from a Taylor-series expansion. On the contrary, we do not assume that any given model adequately describes the dynamics of population growth. Instead, we estimate the approximate linear dynamics about the carrying capacity directly from empirical observations. Because our analysis does not depend on the validity of any given model, we expect our estimated eigenvalues to be more accurate than those based on specific models; for example, Hassell et al. (1976) assume that the equation, $N_{t+1} = \lambda N_t/(1 + aN_t)^\beta$ is valid for a wide variety of species.

Results

The modulus of the largest eigenvalue with its 95% confidence interval is given in Table 1 for each of the 25 lines. Lines 1 to 52 are each homozygous for a different second chromosome sampled from a natural population; H is the random heterozygous line. The result of the one-way analysis of variance (ANOVA) of the eigenvalues is shown at the bottom of the table. Only five of the 25 populations have an eigenvalue with a modulus greater than one and none of these eigenvalues is statistically greater than one at the 5% level of significance. The F statistic from the ANOVA indicates that these populations may be considered as a homogeneous sample with respect to their eigenvalues. The average modulus and 95% confidence interval for all populations is 0.82 ± 0.09. The observation that most eigenvalues have moduli less than or equal to one and that none is significantly greater than one is of considerable consequence; possible evolutionary explanations for this observation will be explored in the Discussion.

TABLE 1. Carrying capacity (K) and modulus of the largest stability eigenvalue (with 95% confidence interval) in each of 25 genetically different populations of *Drosophila melanogaster*. Populations 1 to 52 are each homozygous for a different second chromosome; H is a random-heterozygous population.

Population	Number of replicates	Experimental densities* a	Experimental densities* b	K	Modulus of largest eigenvalue
H	24	500	750	680 ± 13	0.73 ± 0.42
1	9	750	1000	830 ± 20	0.76 ± 0.23
2	9	750	1000	830 ± 22	0.72 ± 0.27
3	12	500	750	720 ± 30	0.84 ± 0.17
6	9	750	1000	1100 ± 53	1.19 ± 0.54
7	12	500	750	611 ± 24	0.48 ± 0.26
8	9	750	1000	880 ± 21	0.96 ± 0.69
9	9	750	1000	900 ± 34	0.87 ± 0.69
13	12	500	750	610 ± 19	0.32 ± 0.43
14	9	750	1000	1000 ± 20	0.93 ± 0.32
15	9	750	1000	720 ± 15	0.96 ± 0.15
18	9	750	1000	1100 ± 24	1.28 ± 0.50
20	9	750	1000	910 ± 24	0.76 ± 0.39
23	12	500	750	690 ± 27	0.87 ± 0.62
25	9	750	1000	770 ± 20	1.08 ± 0.67
30	12	500	750	550 ± 41	0.76 ± 0.30
33	12	500	750	720 ± 18	0.70 ± 0.33
36	9	500	750	650 ± 15	0.50 ± 0.54
37	12	500	750	650 ± 15	0.83 ± 0.14
40	12	500	750	710 ± 21	1.10 ± 0.29
42	9	750	1000	960 ± 41	0.52 ± 0.15
43	12	500	750	610 ± 20	0.81 ± 0.20
45	12	500	750	600 ± 21	0.79 ± 0.08
50	9	750	1000	790 ± 13	1.23 ± 0.67
52	12	250	500	500 ± 24	0.59 ± 0.12
ANOVA results: $F_{23,225} = 1.1961$; $P = .25$					

* Number of adults introduced into the first culture of each line.

The ANOVA result seems, at first, surprising. When populations homozygous for a whole chromosome are examined with respect to properties such as relative fitness (Tracey and Ayala 1974), rate of population growth at different densities (Mueller and Ayala, 1981*c*), and the parameters r, K, and θ from the logis-

tic and the theta models (Mueller and Ayala 1981*a*), the populations exhibit large differences from each other. One possible explanation of the homogenetiy of the eigenvalues is that the homogeneity is only apparent; large differences among the eigenvalues of these populations exist, but we have been unable to detect them. Indeed, the range of the stability eigenvalues is fairly large (0.32–1.28). The relatively large number of parameters estimated in Eq. 2 and the moderate number of replicates (Table 1) may result in estimates of the stability eigenvalues with a much larger variance than that of the other population properties mentioned above.

It is not unreasonable to expect that the collection of more data (more replicates and/or more populations) might uncover significant differences between the stability eigenvalues of these homozygous lines. Nevertheless, the fact remains that in spite of the moderately large number of lines studied, none has an eigenvalue significantly greater than one.

Discussion

Our results add considerable support to the conclusion reached by other authors that most laboratory and natural populations have equilibrium population sizes that are asymptotically stable to small perturbations. Hassell et al. (1976) have estimated the parameters for a single growth equation in a wide variety of species and concluded that most populations should have a stable equilibrium; only one population had an eigenvalue within the chaotic range.

Thomas et al. (1980) have analyzed the stability of many different species of *Drosophila* using the serial transfer system. Their experimental procedures are similar to ours, although their method of analyzing the population dynamics in the serial transfer system is quite different. Their results are, nevertheless, quite similar; most species tested have stable carrying capacities.

One interesting question raised by these results concerns the evolutionary mechanisms that lead so many diverse populations to have stable equilibria. Thomas et al. (1980) suggest that group selection may be the dominant process in the evolution of population stability. They argue that populations with cyclic or chaotic dynamics have a greater chance of becoming extinct; the process of extinction is driven by environmental or demographic stochasticity. Such argument is consistent with Gilpin's (1975) theory of group selection in predator-prey communities. However, the operation of group selection in natural populations encounters severe constraints. It is therefore desirable to advance models, according to which populations evolve stable dynamics as a result of natural selection operating at the individual level. This we do in the following paragraphs.

We restrict our attention to first-order difference equations. One class of such models has been described by Prout (1980). Prout's models are nontrivial reformulations of some standard models and use parameters that explicitly refer to important life-history phenomena. In these models, the life history is considered to consist of two stages: an immature stage and an adult stage. It is assumed that density-dependent regulation acts before the adult stage. The number of immatures at a given time is FN_t, where F is the per-capita fecundity and N_t is the current number of adults. Survival of these immatures to the adult stage is some function of the number of immatures, i.e., $S(FN_t)$. Hence, the first-order difference equation may be written as $N_{t+1} = S(FN_t)FN_t$. The equilibrium population size is achieved when $N_t = K$ and may be determined from $S(FK) = 1/F$. This equilibrium point will be stable if $|\lambda_K| < 1$, where $\lambda_K = 1 + FKS'(FK)$, and S' is the derivative of S with respect to N.

We will examine two models that lead to cyclic and chaotic behavior. These models are the logistic,

$$N_{t+1} = (\tilde{S} - sFN_t)FN_t, \tag{3}$$

and the exponential,

$$N_{t+1} = [\tilde{S} \cdot \exp(-sFN_t)]FN_t. \tag{4}$$

The density-dependent survival functions in Eqs. 3 and 4 have two parameters, $\tilde{S}$ and s. $\tilde{S}$ represents the highest frequency of immatures that survive when densities are very low. The rate at which survivorship decreases with increasing density is determined by the parameter s. For Model 3, $\lambda_K = 2 - F\tilde{S}$ and for Model 4, $\lambda_K = 1 - \ln(F\tilde{S})$. It is apparent that if $\tilde{S}$ is kept constant and F is allowed to increase, then the population will eventually become unstable, because $|\lambda_K|$ will become greater than one and hence the stability criterion ($|\lambda_K| < 1$) will not be satisfied.

As pointed out by Prout (1980) density-independent selection will favor increasing F without any apparent bound. The fecundity of an organism will not, of course, increase indefinitely; there will be some physiological limit. Of greater interest is the possibility that a compromise may be reached between fecundity and some other life-history trait. Density-dependent survival of immatures is another life-history event that may be subject to natural selection in the models under consideration. In Model 3 survival is a linear decreasing function of the number of immatures; the slope of this line is $-s$. It seems reasonable that, at high densities, individuals more tolerant of the density effects would have an advantage and that such individuals would be characterized by a smaller value of s. Further, we may assume that, owing to physiological constraints, genotypes more able to tolerate high densities (low s) may in turn have lower fecundity (F) (see Prout 1980, Fig. 12). A trade-off between life-history parameters has been proposed many times before (e.g., Cody 1966, Roughgarden 1972) and is a crucial assumption to the theory of r- and K-selection. Empirical evidence from populations of *Drosophila mel-*

anogaster supports the existence of such trade-off (Mueller and Ayala, 1981*b*).

In order to explore the evolutionary consequences of a trade-off, we have performed computer simulations with Models 3 and 4. It should be emphasized that the main function of these simulations is to provide counter-examples to the group selection arguments, rather than a general picture of density-dependent selection with cycling or chaotic dynamics. It is not possible to write a simple expression for the equilibrium points of Models 3 and 4. Thus, one can not get the sorts of analytic results that Felsenstein (1979) has recently obtained with a different model. We assume that the parameters F and s of an individual are controlled by a single locus or a tightly linked group of loci. The values of all parameters used in this study were chosen as reasonable approximations for *Drosophila melanogaster* populations kept in standard ¼-L (half pint) cultures in which egg laying is allowed for 1 d. The population starts out fixed for one allele (called the "resident" allele) with F and s values that yield either a two-point cycle or chaotic dynamics. A mutant individual is introduced that is heterozygous for an allele ("introduced" allele) with different values of F and s. This allele may be either dominant or recessive to the resident allele. We then determine whether or not the introduced allele will increase and spread through the population. The simulation actually used two criteria. Evolution was allowed to proceed until either (1) the introduced allele had reached a frequency of 0.99 or greater, or 0.01 of its initial frequency, or (2) 2000 generations had elapsed. Under the second condition a successful allele was simply one that had increased from its initial low frequency. Although criterion 1 was satisfied in many cases, we have only considered whether or not the introduced allele increases when rare. F and s values were chosen so as to determine critical values where the behavior of the alleles changes.

Fig. 1 shows the results for the exponential Model 4. The initial population starts in a two-point cycle. Combinations of F and s above each line represent alleles that are eliminated from the population. Combinations below the line represent alleles that become established in the population. Values of F to the left of the vertical dashed line represent alleles that will yield a stable equilibrium when fixed in the population. $\bar{S}$ is held constant.

The first observation to make is that the mere assumption of a trade-off between F and s is not sufficient to bring a cycling population back to a stable regime. In Fig. 1 the results with respect to the recessive allele (lower curve) are marked by different shadings that delimit critical regions. Region I contains alleles that show severe reduction in F relative to the initial conditions; alleles in this region cannot become established (they are above the solid line). Alleles in region III show large reductions in s, but modest in F, relative to the initial conditions; these alleles become established, but the resulting population will not have a stable equilibrium point. Region II represents alleles that can displace the resident allele and that yield a stable equilibrium. Inspection of Fig. 1 shows that region II will always be larger for dominant than for recessive alleles; in fact, region II for the dominant allele includes all of region II for the recessive allele. Thus the conditions for the evolution out of the cycling regime are broader when the introduced allele is dominant to the resident allele.

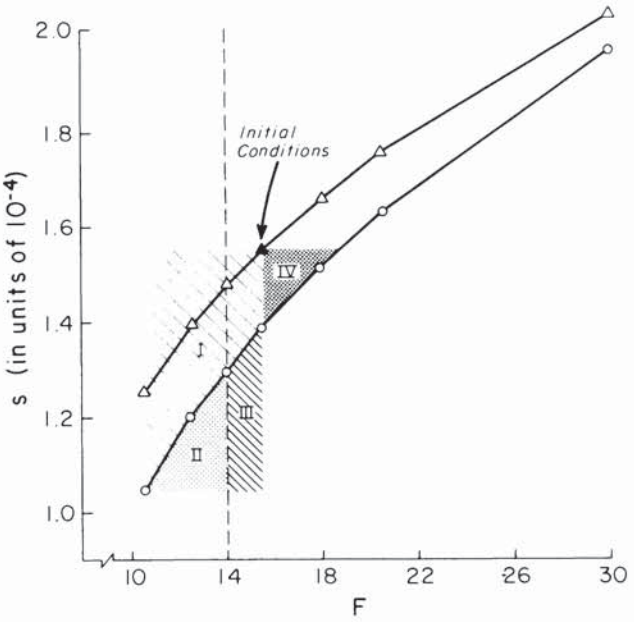

FIG. 1. Evolution of population growth dynamics for the exponential model, given by Eq. 4 in the text. The parameter values of the intial conditions are $F = 15.5$, $s = 10^{-4}$, $\bar{S} = 0.53$. Each solid line divides the plane into two regions; the line with triangles is for dominant alleles, the line with circles for recessive alleles. Introduced alleles are eliminated by natural selection if they have parameter values above the line, but become established if they have parameter values below the line. Regions I, II, III, and IV are defined in reference to the recessive alleles (line with circles). Alleles in both regions II and III are favored by natural selection relative to the initial allele or to any allele above the solid line with circles; alleles in region II yield a stable equilibrium, while those in region III do not.

Of course, if there is no trade-off; alleles with larger F and smaller s are always favored, with one interesting exception. Region IV in Fig. 1 shows alleles with larger F and smaller s than the initial conditions; yet these alleles are eliminated. This region IV does not exist when the introduced alleles are dominant to the established allele.

Fig. 2 shows the simulation results for Logistic Model 3. Two different initial conditions are used. The first condition, with $F = 15.5$ and $s = 10^{-5}$, yields a two-point cycle. The solid lines mark off the successful (below the line) from the unsuccessful (above the line) alleles; the upper line is for the dominant case and the lower line is for the recessive case. The results

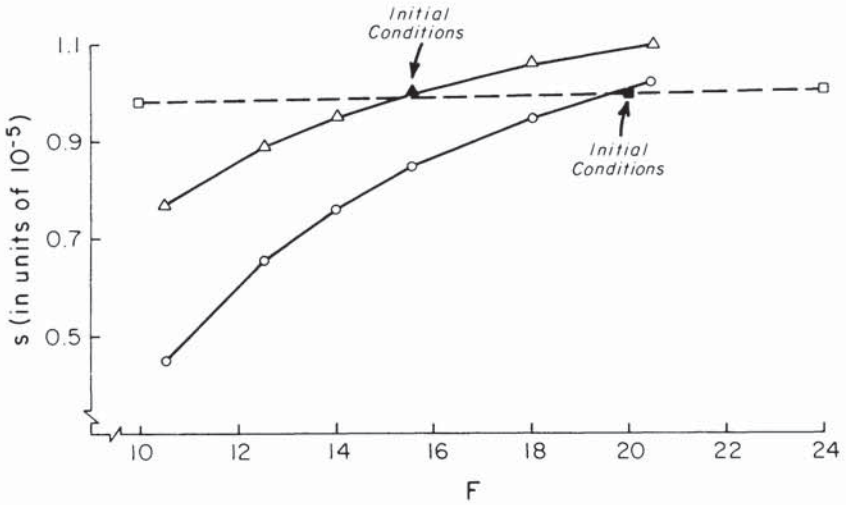

FIG. 2. Evolution of population growth dynamics for the logistic model, given by Eq. 3 in the text. The solid lines are for a population with initial conditions $F = 15.5$, $s = 10^{-5}$, $\bar{S} = 0.20$; the line with triangles is for dominant alleles, the line with circles for recessive alleles. The dashed line is for a population with initial conditions $F = 20$, $s = 10^{-5}$, $\bar{S} = 0.20$. As in Fig. 1, alleles below a given line are favored by natural selection, while those above the line are eliminated.

obtained with a second base population having $F = 20$ are also shown in Fig. 2 (dashed line). The initial population has dynamics that can be described by the logistic equation,

$$N_{t+1} = N_t[1 + r(1 - N_t/K)], \qquad (5)$$

with $r = 3$ (in which case a strange attractor exists, see Guckenheimer et al. 1977). The results given by the dashed line in Fig. 2 are for recessive alleles. For this chaotic population it is obvious that region II has increased at the expense of region I (compare Fig. 2 with Fig. 1, in which the boundary line is lower and bends down further). Thus almost any reduction in s even if it entails a sizeable redution in F will be favored by natural selection in populations that are far out of the stable region.

The most important question, for which we have no data, is what are the combinations of s and F that are physiologically possible. It might be possible to determine such combinations by means of laboratory populations. The experiments would require a genetically heterogeneous base population (of, say, *Drosophila*); many independent samples could be maintained in a discrete system of reproduction for many generations to allow for their evolution. After a suitable period of time, the dynamics of the populations in the discrete regime would be examined in order to obtain estimates of $\bar{S}$, s, and F. If these parameters had also been measured at the start of the experiment, then the changes accomplished by natural selection could be determined. The experimental results presented above show that none of the different *Drosophila* genotypes sampled in our experiments yields an eigenvalue significantly greater than one in the serial transfer system. However, these experimental populations have not evolved for any appreciable time in the serial transfer system.

TABLE 2. Evolution of population stability for two versions of the logistic model in a haploid population. Under the initial conditions (allele A), the population oscillates in a two-point cycle, with densities (1307.53, 2246.19). The two models are given by Eqs. 3 and 5 in the text.

Model	Resident allele (A)	Introduced allele (a)	Does introduced allele increase when rare?
5)	$r_A = 2.30$ $K = 1900.83$ $\lambda_K = 1.3$	$r_a = 1.15$ $K = 1900.83$ $\lambda_K = 0.15$	Yes
Recursion: $N'_A = \left[1 + r_A\left(1 - \frac{N_t}{K}\right)\right] = (1 + r_A)N_A - \frac{r_A}{K}[N_A(N_A + N_a)]$			
3)	$F_A = 110$ $\bar{S}_A = 0.03$ $s = 10^{-7}$ $\lambda_K = 1.3$	$F_a = 77.78167$ $\bar{S}_a = 0.02764147$ $s = 10^{-7}$ $\lambda_K = 0.15$	No
Recursion: $N'_A = N_A F_A[\bar{S}_A - s(F_A N_A + F_a N_a)] = (F_A \bar{S}_A)N_A - sF_A[N_A(F_A N_A + F_a N_a)]$			

Although the computer analysis gives similar results for Models 3 and 4, any general conclusion about the evolution of population stability will be model dependent. Two examples should make this point clear. If we let

$$(F\tilde{S} - 1) = r \text{ and } [(F\tilde{S} - 1)/sF^2] = K, \quad (6)$$

Logistic Equation 5 can be derived, upon simplification, by substituting Eq. 6 into Eq. 3. It is now possible to construct a numerical example where the outcome of evolution will depend on whether Eq. 3 or Eq. 5 is used. The results of the computer simulations are summarized in Table 2. The simulation was carried out with a haploid population using Models 3 and 5. With the help of the identities given in Eq. 6, it can be seen that r and K are identical for both examples in Table 2. However, the new variant is established when the population dynamics are governed by Model 5, but eliminated when they are governed by Model 3. The recursions in Table 2 are not identical to each other once the genetic variants are introduced into the population. The explanation for this difference is that Eq. 3 specifies that the density dependence is a function of the number of immatures, not of the number of adults. Model dependence was also seen in a somewhat different setting by Turelli and Petry (1980).

Another growth equation considered by Prout (1980) is the hyperbolic equation,

$$N_{t+1} = [\tilde{S}/(1 + sFN_t)]FN_t. \quad (7)$$

For this model $\lambda_K = 1 - (\tilde{S}F - 1)/\tilde{S}F$. The inequality $|\lambda_K| < 1$ places the following restrictions on the parameter values, $-1/F < \tilde{S} < 1/F$. These conditions will be satisfied as long as: (1) the carrying capacity is greater than zero, (2) the rate of survival of immatures, $\tilde{S}$, at low density is greater than zero, and (3) the per-capita fecundity, F, is greater than zero. Thus, if the dynamics of a population are governed by Eq. 7, cycling or chaos (which require $|\lambda_K| > 1$) cannot occur with biologically meaningful values of $\tilde{S}$ and F.

Some recent theoretical results (Heckel and Roughgarden 1980, Turelli and Petry 1980) on density-dependent selection in random environments provide predictions consistent with our experimental findings. Turelli and Petry consider models of the form,

$$N_{t+1} = N_t G[(N_t/K)^\theta],$$

where $G(x)$ is one of three different models: $G(x) = \max[0, 1 + r(1 - x)]$; $G(x) = \exp[\ln(1 + r)(1 - x)]$; $G(x) = (1 + r)/(1 + rx)$. Environmental noise is added, in both a density-dependent and -independent fashion, by multiplying G and K by $(1 + Z_t)$ and $(1 + Z'_t)$, respectively, where Z_t and Z'_t are cross-correlated noise terms. When r is held constant and θ is allowed to evolve, Turelli and Petry have shown that natural selection results in parameter values that correspond to stable deterministic dynamics.

The model of Turelli and Petry differs from our computer simulations in that it assumes a random component for the environment and in that the population intially exhibits stable population dynamics. However, their study as well as ours assume that selection acts at the individual level.

The experimental results from our study are clear: the vast majority of *Drosophila melanogaster* populations exhibit stable population dynamics. It is clear that it is not necessary to invoke group selection to explain the results. Future theoretical work must attempt to explain these consistent results. The work of Turelli and Petry is important in providing some unifying theory that is consistent with our, and other, empirical results.

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